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Fine-scale genetic and social structuring in a central Appalachian white-tailed deer herd

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Spatial genetic structure in white-tailed deer (*Odocoileus virginianus*) has been examined at regional scales, but genetic markers with the resolution to detect fine-scale patterns have appeared only recently. We used a panel of microsatellite DNA markers, radiotelemetry data, and visual observations of marked deer to study fine-scale social and genetic structure in a high-density population of white-tailed deer (12–20 deer/km^2). We collected genetic data on 229 adult females, 102 of which were assigned to 28 social groups. Our results were consistent with the conceptual model of white-tailed deer social structure, where philopatric females form social groups composed of related individuals. Within-group relatedness values approached the expected value for 1st cousins ($R = 0.103$, $SE = 0.033$), but individuals among groups ($R = -0.014$, $SE = 0.003$) and overall ($R = -0.009$, $SE = 0.003$) were unrelated. Fixation indices revealed a significant departure from equilibrium values among social groups ($F_{ST} = 0.076$, $SE = 0.007$) and an excess of heterozygotes within groups ($F_{IS} = -0.050$, $SE = 0.018$), consistent with theoretical expectations for mammal populations characterized by female philopatry and a polygynous mating system. Analyses of spatial autocorrelation indicated genetic structuring occurred at a very fine spatial scale, where pairs of adult females within 1 km were genetically nonindependent. The occurrence of fine-scale genetic and social structure has implications for the ecology and management of white-tailed deer, including habitat use and resource competition, offspring sex allocation theories, disease transmission, and the consideration of social behaviors in management. DOI: 10.1644/09-MAMM-A-258.1.

Key words: female philopatry, genetic structure, *Odocoileus virginianus*, relatedness, social groups, spatial autocorrelation, white-tailed deer

Ungulates are large and highly vagile organisms, with the capability to move long distances. Despite this potential for long-distance dispersal, however, genetic structuring is a persistent feature of ungulate populations, where structure can occur as a result of behavior or landscape features that act as barriers to movement. Behavioral attributes that define population structure include dispersal, social behavior, and mating systems. Dispersal in mammals is predominately male-biased, where juvenile or physically immature males disperse from their natal area, but females are philopatric (Greenwood 1980). Many populations of ungulates display a social organization built around social groups composed of female relatives in a polygamous or polygynous mating system (Clutton-Brock 1989). Population genetics theory predicts that the sociobehavioral attributes of ungulate populations, including sex-biased dispersal, social organization, and mating

system, should result in genetic structuring (Chesser 1991). Empirical studies of mammals have confirmed that socio-behavioral attributes result in genetic structuring among a broad range of taxa (Storz 1999). As the acquisition of genetic data from highly variable genetic markers becomes widespread, empirical studies of fine-scale genetic structuring in ungulates are beginning to appear (DeYoung and Honeycutt 2005). Recent studies have found that genetic structuring due to the sociobehavioral attributes of ungulates can occur at finer spatial scales (0.1–1 km) than previously suspected (Coltman et al. 2003; Frantz et al. 2008; Nussey et al. 2005).

White-tailed deer are the most abundant and geographically widespread ungulate in North America (Demarais et al. 2000), yet few studies of fine-scale genetic structure are available. The conceptual model of social organization in white-tailed deer is centered on the formation of matriarchal social groups composed of adult females and several generations of female offspring (Hawkins and Klimstra 1970; Hirth 1977; Mathews and Porter 1993). Members of female social groups associate throughout the year (Aycrigg and Porter 1997; Nelson and Mech 1984), and males are solitary during the breeding season but otherwise aggregate into temporary bachelor groups of nonrelated individuals (Hirth 1977). Rates of female dispersal are typically low (2–20%—Hawkins and Klimstra 1970; Nelson 1993). In contrast, the dispersal rates of males can exceed 70% (Campbell et al. 2005; Rosenberry et al. 2001), with dispersal distances ranging from a few kilometers in heavily forested areas to dozens of kilometers in open habitats (Long et al. 2005).

The sociobehavioral attributes of white-tailed deer are clearly conducive to the formation of genetic structure. Occurrence of genetic structure in populations of white-tailed deer has been confirmed at regional (Leberg and Ellsworth 1999) and local (Blanchong et al. 2006; Cronin et al. 1991; Purdue et al. 2000; Scribner et al. 1997) spatial scales. Studies of fine-scale genetic structure (at spatial scales $<$ 2–5 km) are few, and the conceptual model of spatial organization and fine-scale structuring in white-tailed deer is synthesized from a handful of studies in migratory herds of white-tailed deer occurring at low population density (5–7 deer/km^2 [Mathews and Porter 1993] and $<$0.5 deer/km^2 [Nelson and Mech 1987]). White-tailed deer exhibit a high degree of behavioral plasticity across their range (Miller 1997), including notable exceptions to generalized behaviors, such as female philopatry (Nixon et al. 1991). The occurrence and spatial extent of genetic structure in populations of large mammals has important implications for disease transmission, evolutionary and life-history processes, and behavior-based strategies to alleviate human–wildlife conflicts (Festa-Bianchet and Apollonio 2003). Thus, information on fine-scale genetic structure in a greater number of populations will have clear implications for the ecology and management of white-tailed deer.

Our overall objective was to examine the fine-scale genetic structure in a free-ranging white-tailed deer herd in the eastern United States. We used data from radiotelemetry and 14 microsatellite DNA loci to test for fine-scale genetic structure among adult females, describe the spatial extent of fine-scale genetic structure, and assess the role of female social groups in fine-scale structure.

Materials and Methods

Study area.—Our research was conducted on the 3,413-ha MeadWestvaco Wildlife and Ecosystem Research Forest located in Randolph County, West Virginia (38°42′N, 80°3′W). The MeadWestvaco Wildlife and Ecosystem Research Forest was established in 1994 to investigate the relationship between industrial forestry and ecosystem processes. The MeadWestvaco Wildlife and Ecosystem Research Forest is located in the unglaciated Allegheny mountain and plateau physiographic province, and topography consists of plateaulike ridgetops with steep sides and narrow valleys (Smith 1995). Elevations range from 700 to 1,200 m. The climate is moist and cool with mean annual precipitation in excess of 155 cm (Strausbaugh and Core 1977). The most common forest overstory cover is Allegheny hardwood–northern hardwood type composed mainly of American beech (*Fagus grandifolia*), birch (*Betula* spp.), black cherry (*Prunus serotina*), maple (*Acer* spp.), and yellow-poplar (*Liriodendron tulipifera*). The proportion of the study site composed of forest regeneration areas $\leq$ 10 years of age increased from 8% to 14% during the study. Deer densities and sex ratios on the MeadWestvaco Wildlife and Ecosystem Research Forest during the study were estimated as 12–20 deer/km^2 and 6–18 adult males : 100 adult females, respectively (Langdon 2001). Males experienced high annual mortality from hunting, whereas females averaged 85–90% annual survival (Campbell et al. 2005). Radiotelemetry data from a previous study revealed low levels ($<$5.0%) of dispersal in juvenile females (Campbell et al. 2004a). Abomasal parasite counts indicated the deer herd was near nutritional carrying capacity (Fischer 1996). Overall, this nonmigratory, high-density white-tailed deer herd in the central Appalachian Mountains is characteristically representative of many populations in the eastern United States.

Deer capture and tissue sample collection.—We captured deer from 27 February 1999 to 19 March 2005 using Clover traps (Clover 1954) baited with whole-kernel corn. Deer had compact home ranges, requiring us to deploy traps widely throughout the area to ensure broad coverage. We used $>$100 sites dispersed throughout the area, facilitated by a large network of primitive logging roads. We trapped each site on a short-term (1- to 2-week) basis, and traps were moved to a new location when trap success declined. Captured animals were physically restrained, blindfolded, and given an intramuscular injection of xylazine hydrochloride (100 mg/ml, Cervizine; Wildlife Laboratories Inc., Fort Collins, Colorado) at a dosage of 2.2 mg/kg body mass. We affixed large numbered plastic ear tags (National Band and Tag Co., Newport, Kentucky) and estimated the age of immobilized animals via tooth wear and replacement (Severinghaus 1949). We collected whole blood or ear-notch tissue from captured

deer and muscle tissue samples from fetuses obtained from deer euthanized for additional research purposes. We combined blood samples (2 ml) obtained via jugular venipuncture with 6 ml of Longmire's solution (Longmire et al. 1997) in Vacutainer tubes (Benton Dickinson, Franklin Lakes, New Jersey). We stored the blood–lysis buffer samples at room temperature. We immediately placed ear-notch and muscle tissue samples in Vacutainer tubes (Benton Dickinson) containing 8 ml of 95% ethanol and allowed samples to fix at 4°C for ≥24 h. We then stored tissue samples at room temperature. We outfitted captured animals with very-high-frequency radiocollars (Advanced Telemetry Systems, Isanti, Minnesota). We reversed immobilization with a 12.0-mg intramuscular injection of yohimbine (5 mg/ml, Antagonil; Wildlife Laboratories, Inc.). Capture and handling procedures were consistent with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Collection of radiotelemetry data.—We located radiocollared animals ≥2 times per week throughout the 24-h day from permanent georeferenced telemetry stations ($n = 591$) during April 1999–April 2005, allowing ≥10 h between telemetry locations. We used 4-element yagi antennas and radioreceivers (Advanced Telemetry Systems) to estimate deer locations. We collected 3–8 preliminary azimuths to pinpoint deer locations and recorded 2 simultaneous azimuths that yielded an angle of $90^\circ \pm 40^\circ$. We used the LOCATE function of the computer program CALHOME to generate Universal Transverse Mercator coordinates of deer locations (Kie et al. 1996). We calculated distances between home-range centers of individuals determined by the harmonic means of telemetry locations (Animal Movement extension version 2.04—Hooge and Eichenlaub 1997) using the computer program Arcview GIS 3.3 (Environmental Systems Research Institute 1999). The coordinates from trap-site locations obtained via a submeter global positioning system (GeoExplorer 3; Trimble Navigation Limited, Sunnyvale, California) were used for individuals lacking telemetry data. To estimate telemetry error we placed radiocollars at random georeferenced sites in areas commonly used by deer (Samuel and Fuller 1996). Each researcher recorded an azimuth to a radiocollar from 5 telemetry stations, resulting in a mean bearing error of -0.65° ($SD = 8.41^\circ$).

Delineation of social groups.—We recorded opportunistic visual observations of marked and unmarked animals along roadsides during April 1999–April 2005 using 10 × 40 binoculars. Our observational data included date and time of observation, nearest georeferenced telemetry station, sex, age class (juvenile or adult), size of group, and ear-tag numbers of marked animals. We considered individuals separated by ≤25 m and moving in a coordinated fashion to be associating (Aycrigg and Porter 1997). We considered marked animals members of a social group if animals were visually observed associating together on a minimum of 60% of occasions where putative group members were sighted, and were observed as an intact group ≥2 times. Juveniles were not considered members of a social group until ≥18 months of age. We assigned each social group a spatial location representing the estimated center of the group's range based on visual observations and telemetry locations.

DNA extraction and amplification.—We extracted total DNA from samples using a Qiagen DNeasy Blood and Tissue Kit (Qiagen, Inc., Valencia, California). We selected a panel of 14 microsatellite loci from the 21 identified for use with white-tailed deer (Anderson et al. 2002; DeYoung et al. 2003). The BM145, BM203, BovPRL, ETH152, K, OCAM, and R loci were omitted. We amplified DNA fragments by polymerase chain reaction following Anderson et al. (2002). We mixed the polymerase chain reaction products with an internal size standard (GeneScan-500 [ROX]; Applied Biosystems, Foster City, California) and loaded the mixture on an ABI PRISM 3130 Genetic Analyzer (Applied Biosystems) for separation and detection. We binned and assigned alleles using GeneMapper software (Applied Biosystems) followed by visual inspection and verification.

We used the identity analysis function of the computer program CERVUS 2.0 (Marshall et al. 1998) to detect duplicate genotypes that could have been caused by the inadvertent resampling of deer with missing ear tags. We performed the identity analysis using the fuzzy matching option, where individuals sharing up to 3 mismatching alleles were flagged. We also performed tests for Hardy–Weinberg equilibrium, and estimated allelic diversity, and expected and observed heterozygosity.

Spatial genetic structure.—We performed an analysis of spatial autocorrelation to test for fine-scale genetic structure and investigate the spatial extent of genetic structure in the study area. Spatial autocorrelation quantifies the degree to which individual genotype frequencies are correlated as a function of the Euclidian geographic distance between pairs of individuals (Manel et al. 2003). Spatial autocorrelation analysis can be especially useful to summarize genetic variation for populations that are distributed continuously (Dinez-Filho and Telles 2002). We used Moran's I (Moran 1950; Sokal and Oden 1978) as a measure of autocorrelation because the performance of, and theoretical basis for, Moran's I has been investigated extensively in simulation and empirical studies (Epperson 2004; Hardy and Vekemans 1999). For each pairwise comparison between individuals at a locus the correlation is 0, 0.5, or 1.0, depending on whether the 2 individuals share 0, 1, or 2 alleles; the individual locus correlations are averaged to obtain an overall value of I. Moran's I (averaged over loci) was taken for all pairs of individuals separated by geographic intervals of 200 m. Only adult females (aged ≥1.5 years) were included in the analysis. We tested the statistical significance (2-sided) of Moran's I for each 200-m distance class by comparing the observed value versus a null value derived from 10,000 permutations of individual locations. We estimated standard errors of I-values by jackknifing over loci.

We performed additional analyses to assess the importance of social groups to spatial genetic structure on the study area and to determine if groups were composed of female relatives.

All analyses based on social groups included only adult (≥1.5 years old) females. First, we repeated the autocorrelation analyses with social groups as a categorical variable, where pairwise comparisons between members of the same group were not included. Similar to the procedure described above, we used Moran's *I* as the autocorrelation coefficient, and we assessed statistical significance by 10,000 permutations of spatial locations. We increased distance intervals from 200 m to 500 m to ensure that >100 pairs occurred within each distance class, ensuring precision of estimated *I*-values. We also derived global estimates of genetic structure by calculating Weir and Cockerham's (1984) modification of Wright's F_{IT}, F_{IS}, and F_{ST} (Wright 1978), where social groups were considered as subpopulations. Statistical significance was assessed by 10,000 permutations of genes among individuals (for F_{IS} and F_{IT}) and individuals among social groups (for F_{ST}). Finally, we estimated average relatedness among individuals at 2 levels: pairs of individuals within groups and pairs of individuals among groups. Relatedness can be estimated from genetic data by computing a relationship coefficient, defined as the proportion of alleles in 1 individual identical to those in a reference individual. We used the relationship coefficient *R* of Queller and Goodnight (1989) as an estimate of relatedness and assessed statistical significance by 10,000 permutations of individuals among social groups. We performed all analyses of autocorrelation, population structure, and relationships using the computer program SPAGeDi 1.2 (Hardy and Vekemans 2002).

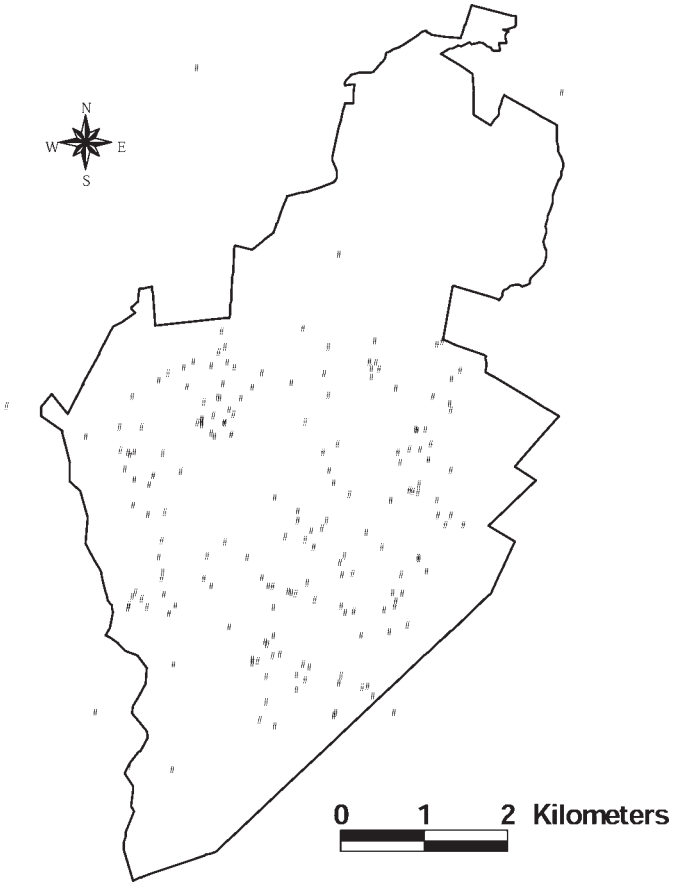

Fig. 1.—Spatial locations (black dots) of 229 adult (≥18 months of age) female white-tailed deer on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, from 1999 to 2005, used in spatial autocorrelation analysis. The solid line represents the boundary of the study area.

Results

We obtained tissue samples from 230 adult females. The identity analysis revealed that 1 female had been sampled twice due to loss of ear tags, leaving 229 individual adults for analyses. Precise density estimates are difficult in heavy forest cover, but we estimate that we sampled about 50% of adult females on the area.

The spatial coordinates used in the analysis were derived from telemetry locations for 139 of the individuals and from capture sites for the 90 other individuals (Fig. 1). Mean (± *SE*) number of telemetry locations per individual was 219.9 ± 13.3. Adult female home ranges in this high-density herd were compact, encompassing about 82 ha (Campbell et al. 2004a). We recorded 17,731 visual observations of deer during the study period, of which 2,831 observations were of identifiable (marked and positively identified) individuals. From these data, we delineated 28 putative social groups containing 102 marked adult (≥1.5 years old) females. Social groups contained a mean (± *SE*) of 3.6 ± 0.5 adult females (range: 2–12 adult females). We never observed radiomarked individuals to change groups. Groups maintained home-range fidelity among years, and only 4% of females had distinct seasonal ranges (6 of 148 radiomarked deer—Campbell et al. 2004a, 2004b). Examination of telemetry data indicated that female home ranges were compact, did not change in response to bait, and females used no bait sites > 100 m outside of the established home range.

The 14 microsatellite loci were highly polymorphic in the study population (Table 1). The number of alleles per locus ranged from 4 to 20, with a mean of 13.2. Mean expected heterozygosity for all loci was 0.781; we detected no deviations from Hardy–Weinberg equilibrium. Statistical power for spatial autocorrelation analyses can be indexed by the total number of alleles multiplied by the number of sampled individuals; if the product is at least several thousand, tests for *I* have sufficient power (Epperson 2005). Thus, our sample of 229 deer and 185 alleles should provide more than adequate statistical power to detect departures from equilibrium. Autocorrelation coefficients revealed statistically significant positive autocorrelation over the 1st five 200-m distance classes and a separate class for individuals with proximate spatial coordinates (e.g., sampled at the same trap site; Fig. 2). Autocorrelation values became nonsignificant by the 6th distance class; average pairwise spatial distances within classes 5 and 6 were 901 and 1,101 m, respectively, suggesting an intercept at about 1,000 m. Six additional statistically significant, negative *I*-values spanned distance

Table 1.—Locus name, number of individuals typed (*n*), number of alleles, observed heterozygosity (H_O), and expected heterozygosity (H_E) for 14 microsatellite DNA loci amplified in 229 white-tailed deer sampled in the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, during 1999–2005.

Locus	*n*	Alleles	H_O	H_E
BL25	228	4	0.408	0.411
BM4208	199	20	0.920	0.923
BM6438	221	16	0.814	0.880
BM6506	226	15	0.858	0.873
BM848	203	14	0.778	0.876
Cervid1	220	16	0.832	0.860
D	223	11	0.767	0.806
ILSTS011	178	7	0.545	0.579
INRA011	223	8	0.552	0.544
N	218	20	0.853	0.912
O	224	8	0.647	0.643
OarFCB193	176	13	0.909	0.882
P	220	14	0.850	0.854
Q	226	19	0.819	0.897

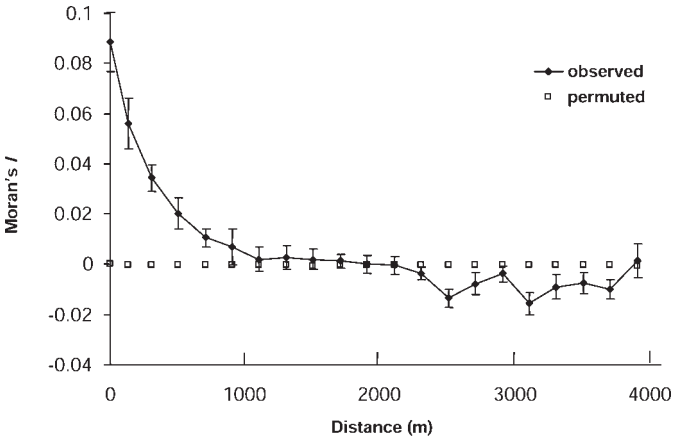

Fig. 2.—Mean (± *SE*) spatial autocorrelation coefficients (Moran's *I*) based on 14 microsatellite DNA loci averaged over 21 spatial distance classes for 229 adult (≥18 months of age) female white-tailed deer at the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, sampled during 1999–2005. The 0.0 distance class included individuals with the same spatial coordinates (i.e., same trap site). A permuted (null) value derived by permutations of spatial distance coordinates among individuals averages near 0.0 for each distance class.

classes 2,600–3,800 m (Fig. 2), suggesting an isolation-by-distance pattern.

When we repeated autocorrelation analyses incorporating social groups, the exclusion of within-group comparisons and individuals not assigned a social group produced a similar correlogram (Fig. 3). However, the slope of the spatial–genetic relationship appeared to decay somewhat faster, where the autocorrelation values became nonsignificant after the first 500-m distance class (Fig. 3). Three additional statistically significant autocorrelation values were observed at greater geographic distances, a positive value at 2,000 m, followed by a negative value at 3,000 m and a positive value at 4,000 m. The mean relationship coefficient for individuals within social groups was 0.103, approaching the expected value for 1st cousins (0.125); a 95% confidence interval for our observed value contains 0.125. In contrast, the mean relationship coefficients among groups and overall were slightly negative (Table 2).

Analyses of genetic structure revealed statistically significant departures from equilibrium values. Estimates of F_{IT} and F_{ST} were positive, indicating a deficit of heterozygotes at the population level ($F_{IT} = 0.030$, $SE = 0.013$, $P = 0.021$) and moderate differentiation among social groups ($F_{ST} = 0.076$, $SE = 0.007$, $P < 0.001$). We observed a negative F_{IS}-value, reflecting an excess of heterozygotes within groups ($F_{IS} = -0.050$, $SE = 0.018$, $P < 0.001$).

Discussion

We used spatial locations and genetic data to describe the spatial pattern of genetic structure on the study site. Some errors in the spatial coordinates for individual deer likely were present due to such factors as use of trap-site coordinates for nonradiomarked deer and telemetry errors. The autocorrelation analysis does account for some uncertainty in spatial locations by pooling many pairwise comparisons into distance classes to ensure a reliable estimate of autocorrelation for each distance class. However, the use of inexact spatial coordinates would only weaken estimates of spatial structure, not create a pattern where none existed. The permutation tests indicate that spatial patterns are very unlikely to arise by chance in this data set. Our bait sites were temporary and dispersed widely throughout the study site, limiting the opportunity for attracting multiple social groups to a site. If baiting influenced use (and resultant structure) by deer on the area, the effect would be to reduce estimates of population structure by attracting deer from multiple social groups (Blanchong et al. 2006); baiting is unlikely to create structuring where none exists. We detected a clear pattern of nonrandom spatial association among females, evidence that the underlying correlation is real and not influenced by capture methods or baiting.

We might have made errors in the assignment of individuals to social groups. White-tailed deer prefer dense cover (Demarais et al. 2000), making behavioral observations difficult to acquire. Furthermore, the home ranges of social groups overlapped on the study area, so we could not use a criterion of home-range overlap to define groups. To mitigate for this we compiled an extensive data set of visual observations to delineate social groups, ensuring that deer in social groups associated socially. We defined social groups only where >1 individual was marked and where repeated sightings were available. Nevertheless, errors of group assignment would only weaken group *R*-values, estimates of fixation indices, and spatial structure. We observed low levels of female dispersal (<5%), high and statistically significant within-group *R*-values, fine-scale structuring, and fixation indices consistent with theoretical expectations (Storz 1999).

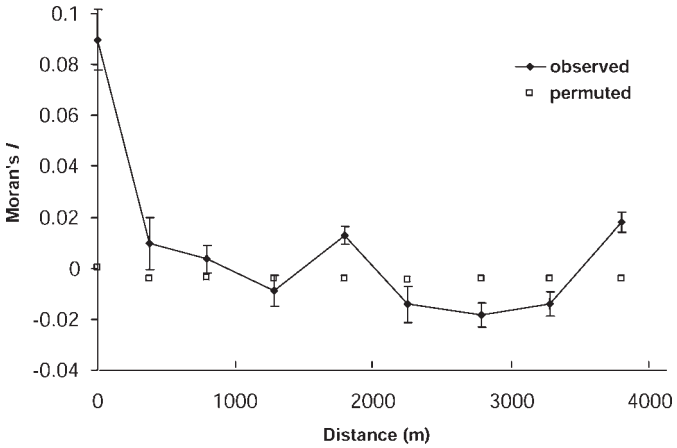

Fig. 3.—Mean (± *SE*) pairwise relationship coefficients (Moran's *I*) by distance between members of 28 social groups (102 adult females) delineated by visual observations on the MeadWestvaco Wildlife and Ecosystem Research Forest, Randolph County, West Virginia, during 1999–2005. The 0.0 distance class is the average *I*-value within social groups. A permuted (null) value derived by permutations of spatial distance coordinates among individuals averages near 0.0 for each distance class.

Overall, our results support the conceptual model of white-tailed deer social organization, where groups are composed mostly of female relatives. Spatial autocorrelation analyses indicate the occurrence of fine-scale genetic structure in this continuously distributed, high-density population of white-tailed deer. The collection of visual observations allowed delineation of social groups on our study area, one of the few studies of white-tailed deer where the role of group membership in genetic structuring was assessed explicitly. Social groups appeared to be the integral components of fine-scale structuring, a conclusion supported by departure from equilibrium values for fixation indices and a positive relationship coefficient for individuals within groups. Significant differentiation among social groups coupled with an excess of heterozygotes within groups is consistent with the generalized mammalian model of philopatric females in a polygynous mating system (Storz 1999).

A comparison of fine-scale structure among 2 populations of ungulates suggested a relationship between home-range size and the spatial extent of fine-scale genetic structure (Coltman et al. 2003; Nussey et al. 2005). We observed a compelling parallel between individual home-range size and the spatial extent of genetic structure on our study area. The mean summer home-range size of adult females on our study area was approximately 82 ha (Campbell et al. 2004b); the diameter of a circular home range of 82 ha was about 1 km, the estimated spatial extent of autocorrelation. Home-range size of adult female white-tailed deer on our study area is near the lower end of reported home-range sizes for female white-tailed deer (range: 45–747 ha—Demarais et al. 2000). Therefore, if home-range size influences the spatial scale of genetic structure, the extent of fine-scale structure might vary extensively throughout the range of white-tailed deer.

Table 2.—Mean pairwise relatedness (*R*—Queller and Goodnight 1989) within group, among group, and overall for 28 social groups of adult female white-tailed deer in the Appalachian Mountains of West Virginia, 1999–2005.

Category	*R*	*SE*	95% confidence interval
Within social groups	0.103	0.033	0.038, 0.168
Among social groups	−0.014	0.003	−0.020, −0.008
All pairwise comparisons	−0.009	0.003	−0.015, −0.003

The spatial scale of genetic structure (≤1 km) we observed is similar to that of a population of cervids with defined matriarchal structure but comparatively larger group sizes than white-tailed deer (Nussey et al. 2005). Our analyses indicate a clear role for social groups in fine-scale genetic structure. When autocorrelation analyses were restricted to comparisons among groups, we observed significant autocorrelation at 500 m. The spatial–genetic relationship appeared to decay at a faster rate than when all pairwise comparisons were included, but nevertheless, social groups did not explain all of the observed autocorrelation. This could be attributed to incomplete or erroneous assignment of individuals into social groups. However, an alternative explanation is that social groups or related individuals in different social groups can overlap in space. Mathews (1989) proposed that the spatial organization of females within social groups in white-tailed deer begins with a series of juvenile female home ranges overlapping the home range of an older female relative. This theory of social group structure implies that the spatial area occupied by a social group will expand outward with each new female added, eventually forming new groups via fissioning of existing groups (Mathews et al. 1997). Thus, the observation of significant autocorrelation during among-group analyses appears consistent with conceptual models of social organization and social group formation in white-tailed deer. The occurrence of sporadic positive autocorrelation values at greater spatial distance classes also might indicate group fissioning, although we cannot verify if this is the case.

Although our results are consistent with the conceptual model of social group structure in white-tailed deer, other studies have found conflicting results. Possible explanations for discrepant results regarding the presence of social and fine-scale genetic structure in white-tailed deer include behavioral responses to disturbance of population age structure or habitat. Aycrigg and Porter (1997) hypothesized that the expected sociospatial behavior in white-tailed deer is dependent on the ability of a population to develop a complex age structure. Female deer on our study site have high annual survival (85–90%—Campbell et al. 2005) and low rates of dispersal (<5.0%—Campbell et al. 2004a), requisite for the development of an age-structured female population. Therefore, departures from age structure or group fidelity probably affect patterns of spatial genetic structure in female white-tailed deer. For instance, studies of exploited populations of white-tailed deer, where rates of female harvest are high, have revealed a low degree of spatial genetic structuring (Comer et

al. 2005; Scribner et al. 1997). A lack of expected fine-scale genetic structuring may be attributed to a young female age structure as a result of intense hunting pressure; if females are harvested at young age, groups composed of different-aged relatives are not able to form.

The effects of intense harvest on female dispersal and social group dynamics are fertile ground for future research, because few data are available. However, white-tailed deer are social animals, and any disruption of family groups due to harvest could promote the association of unrelated females (Williams et al. 2008), disrupting spatial genetic structure. One would also predict that spatial genetic structure is absent in agricultural areas of the midwestern United States, where habitat fragmentation apparently results in high rates of dispersal among juvenile and adult white-tailed deer females (Nixon et al. 1991).

Sociobiology could influence the evolutionary trajectory of populations through interactions within and among groups at local scales, resulting in the coevolution of behavior and gene dynamics (Dobson 1998; Dobson and Zinner 2003). Therefore, the occurrence of fine-scale genetic and social structure has clear implications for habitat use and resource competition (DeRoos et al. 2009), offspring sex allocation theories (Hardy 1997), models of disease transmission (McDonald et al. 2008), and the consideration of social behaviors in conservation and management (Festa-Bianchet and Apollonio 2003; Porter et al. 1991). As more studies accumulate, our understanding of fine-scale genetic and social structure in white-tailed deer and other ungulates continues to grow. Remaining unknowns include how ungulate sociobiology and resultant fine-scale genetic structure might be influenced by habitat structure and population density, and the dynamics and formation of social groups.

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